Reference: *Biol. Bull.*, **142**: 49–56. (February, 1972)

# CAPTURE-RECAPTURE METHODS WITH *UCA*[1]

JOHN C. HOCKETT AND HENRY KRITZLER

*Department of Science Education and Department of Oceanography, Florida State University, Tallahassee, 32306*

A persistent problem in estimating animal population size is the choice of sampling and statistical methods appropriate to the behavior of the species under study. While censuses and controlled areal sampling estimates are suitable for sessile species, capture-mark-recapture methods may be used with mobile species. The maximum-likelihood index usually attributed to Lincoln (1930) and its well-known extensions by Jackson (1937, 1939) take the ratio of the marked and released animals to the total population to be equal to that of recaptured marked animals to the whole of the second capture. They share the assumptions that the marked animals immediately and randomly disperse into the population, that marked animals do not lose their marks, and that both marked and unmarked individuals are equally likely to be captured, marking and handling having no effect on viability or behavior. While the Lincoln Index requires a closed population, Jackson's two models allow for changes in population size during the period of sampling and provide for their specification as to deaths, births, emigration or immigration. Sampling differs in that the Lincoln Index is based on but one capture-mark-recapture sequence while Jackson's "positive" model employs a single marking followed by a series of recaptures and his "negative" method, a series of markings and a single, final recapture.

Casual observations on the behavior of sand fiddler crabs, *Uca pugilator* (Bosc) led us to the speculation that marked individuals might randomly disperse among the unmarked rapidly enough to permit an accurate estimate of population size by the Lincoln Index.

## *The sand fiddler as a test animal*

The behavior of *Uca pugilator* is characterized by a cycle integrated with the stages of the tide. It is divisible into an active and an inactive phase. The active phase, on warm, clear days, occurs on the ebb tide and is made manifest by emergence from the burrows and promenading on the flats. During the inactive phase, which is triggered by the advance of the flood, the crabs retreat to burrows which, when the tide is high, may be covered with sand.

*Uca pugilator* is adapted to a different substrate than that of *U. rapax* (Smith), (Miller, 1961), the mud fiddler of Florida west coast, and can be easily distinguished from it in the field (Tashian and Vernberg, 1958). The sand fiddler is found in intertidal sandy shores sufficiently protected from wave action as to lack the properties of beaches. These often grade laterally into or may be

[1] Contribution No. 279 of the Department of Oceanography, Florida State University.

surrounded by mud flats, and may be bounded on the landward side by salt marshes. These transitions form natural boundaries which ensure the discreteness of the sand fiddler populations.

Crane (1943, 1958) has described the tidal activity cycle of *Uca* species in detail. As the tide retreats, the burrows are cleaned and repaired; desultory ambulation, feeding, and mobbing follow. Near low tide, the mobs promenade, a group activity which may include feeding or may be preliminary to sexual display, courtship, and mating. Individuals may not participate in all phases of activity on any given tide, but all enter burrows on the flood and only a few refrain from joining the promenading mob to engage in other activities.

The mobbing phase of the sand fiddler's activity cycle seems, as we have noted, to be characterized by a randomness of movement which meets the primary assumption of the Lincoln Index, thereby overcoming the most usual stumbling block to its application. In the immobile burrowing phase, on the other hand, there seem to exist conditions suitable for population size estimates by controlled random areal sampling. It is the purpose of this paper to report the results of application of the Lincoln Index to a population of sand fiddlers, the results being compared with those obtained with the Jackson models applied also to the promenading mobs, and with sampling of the population during the immobile phase.

## Methods and Results

### *The study area*

The seaward side of a sand spit lying between a salt marsh and an estuary in Wakulla County, Florida was chosen as the study area. The strand was 285 meters long at the high tide mark and varied in intertidal width from 4.1 to 7.2 meters. Its crest lay about 20 cm above the mean high water mark of spring tides. The tidal range was about 50–70 cm. The sediment consisted largely of medium fine sand with some shell hash and approximately 19% silt. The shoreward 2 or 3 meters of the intertidal were covered with *Spartina alterniflora* which was most densely distributed near the high water mark. The crest was loose sand covered with *Spartina patens* and the high water bush, *Iva frutescens*. At one end, the shore curved back into the *Juncus-Spartina* salt marsh along the high water line, but at low tide a northward projecting sand spit (Fig. 1 (6)) was laid bare. The habitat was chosen from many because of: (a) manageable size, (b) the presence of an apparently isolated population of sand fiddlers, and (c) accessibility.

### *Sampling*

An initial plan to sample randomly during the mobile phase without subdividing the habitat was abandoned when it was noted that the population was already divided in two ways. First, a portion of the spit of about 315 $m^2$ was separated from the rest by an asphalt boat ramp which the fiddlers never cross (Fig. 1, A). Secondly, the population residing in the remainder was naturally subdivided into three mobs which regularly promenaded in clearly defined areas (Fig. 1, B, C, D). Color coded marking eventually showed that only three crabs were found outside their herding territories. This extremely contagious dispersion during the mobile phase called for restricted, or stratified, rather than simple random sampling.

Plastic pans (dimensions: 26 × 33 × 12 cm) were buried, rims flush with the sand surface, about two hours before ebb tide. Neither baiting nor driving was necessary; the normal activity of the mob caused some of the crabs to fall into the pans. The captured crabs were taken up at dead low water. Individual catches ranged between 185 and 567 crabs per pan. The carapaces were dried and marked with acrylic enamel, date and territory of capture being color coded.

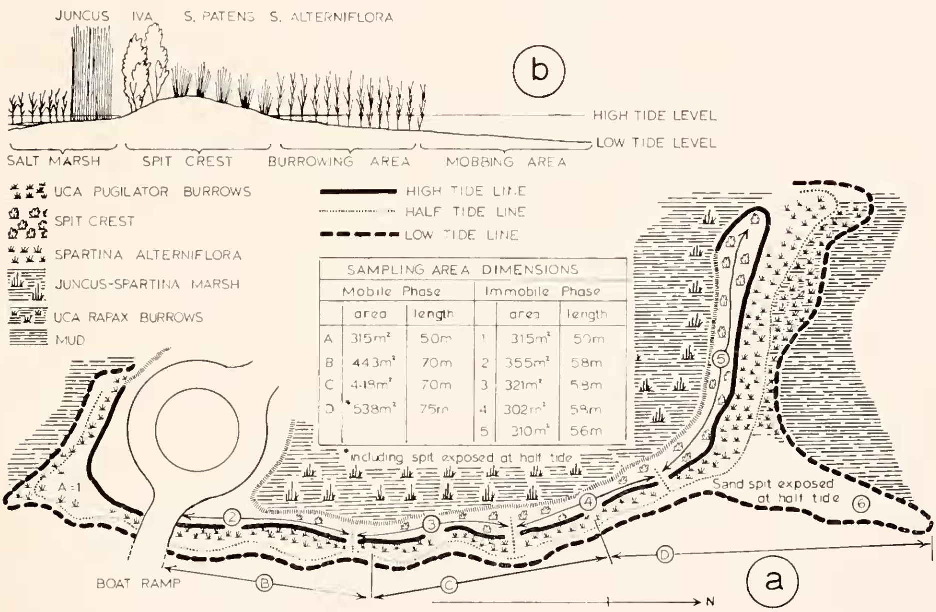


FIGURE 1. The study area. (a.) Plan of the sand spit shows areas sampled during the mobile phase (A, B, C, D) and areas sampled during the immobile phase (1, 2, 3, 4, 5) (not drawn to scale). (b.) Cross section of the sand spit shows the distribution of vegetation and the relationship between tide levels and activity areas of *Uca pugilator* (not drawn to scale).

The marks stood up best when placed near the posterior margin and could be seen clearly from a distance of five meters after three months. No modification of behavior was noted in marked crabs either immediately after release or during subsequent mobile activity phases. Immediate dispersal of the marked among unmarked members of the herd was observed in every case. Processing the catches always left ample time for dispersal into the mob before return to the burrows was triggered by the rising tide.

Samples were taken during the mobile phase on seven consecutive days—October 2 through 8, 1970—at the same relative time of the second or daylight tidal cycle. Data for the Lincoln Index were drawn from captures of those marked the previous day, while continuing mark-recapture data over the entire period were used in applying the Jackson models. In the analysis, the samples for all areas were combined in order to estimate the size of the whole population.

For random sampling during the immobile phase, the burrowing area was divided into five strata (Fig. 1, (1–5)), the boundaries of which were not all coincident with the apparent boundaries of the herding territories. Within each stratum, 1 $m^2$ quadrats were taken at random during the first half of the falling

TABLE I

*Captures and recaptures of* U. pugilator, *October 2 through 8, 1970*

| Date and No. marked | | Date recaptured | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Oct. 3 | Oct. 4 | Oct. 5 | Oct. 6 | Oct. 7 | Oct. 8 | Total |
| Oct. 2 | 513 | 13 | 12 | 8 | 18 | 13 | 11 | 75 |
| Oct. 3 | 1688 | | 30 | 38 | 60 | 41 | 38 | 207 |
| Oct. 4 | 1079 | | | 22 | 34 | 27 | 23 | 106 |
| Oct. 5 | 1570 | | | | 46 | 40 | 40 | 126 |
| Oct. 6 | 1800 | | | | | 42 | 40 | 82 |
| Oct. 7 | 1459 | | | | | | 32 | 32 |
| Oct. 8 | 1371 | | | | | | | |
| Total recaptures | | 13 | 42 | 68 | 158 | 163 | 184 | 628 |
| Total captures | | | | | | | | 8967 |

tide. Most quadrats were dug out to a depth of no new captures, usually about 50 cm or the low-tide level. Sample size was based on plotting cumulative density against quadrat number. When the curves levelled off, signifying that further sampling would yield no additional information, sampling was stopped. These density data were dealt with collectively for the entire sand spit.

## *Results*

Any mark-recapture data pair found in Table I may be used to estimate population size by the Lincoln Index. Taking, for example, the data from 10/2 and 10/3, we have

$$P = \frac{M \times C}{R} = \frac{513 \times 1688}{13} = 66611$$

The succeeding five data pairs yielded: 10/3–10/4: 60711; 10/4–10/5: 77001; 10/5–10/6: 61435; 10/6–10/7: 62529; 10/7–10/8: 62509.

In Table II, the data "corrected" to what they would be if 100 individuals had been captured and marked on each successive day are presented together with products computed to extrapolate back to the start of the experiment. The reader is referred to Jackson's papers (1937, 1939) or to Andrewartha (1961) for the computational methods.

TABLE II

*Values for y, r, $a_0$ and $P_0$ for Jackson's positive and negative models (after Andrewartha, 1961)*

| Date marked and released | Date recaptured | | | | | | r+ | $a_0$ | P pos. |
|---|---|---|---|---|---|---|---|---|---|
| | 10/3 | 10/4 | 10/5 | 10/6 | 10/7 | 10/8 | | | |
| 10/2 | 0.150 | 0.216 | 0.099 | 0.195 | 0.173 | 0.156 | 0.988 | 0.183 | 54644 |
| 10/3 | | 0.165 | 0.143 | 0.198 | 0.166 | 0.164 | 1.023 | 0.150 | 66666** |
| 10/4 | | | 0.129 | 0.175 | 0.171 | 0.155 | 1.053 | 0.147 | 68027 |
| 10/5 | | | | 0.162 | 0.174 | 0.186 | 1.071 | 0.152 | 65789 |
| 10/6 | | | | | 0.159 | 0.168 | 1.018 | 0.156 | 64102* |
| r − | | 1.301 | 0.890 | 1.061 | 1.020 | 1.000 | | | |
| $a_0$ | | 0.126 | 0.177 | 0.167 | 0.153 | 0.160 | | | |
| P neg. | | 79365* | 56497 | 59880 | 65359 | 62500** | | | |

* Values obtained using $r = y_n/y_{(n-1)}$.
** The two most reliable estimates.

From 85 one-square-meter quadrat sample units containing a total of 3472 crabs taken from burrows in an area of 1603 $m^2$, the population density was estimated to be 40.85 crabs/$m^2$ and the population size, 65483 individuals.

## DISCUSSION

An indicator of the relative precision of the methods used here is the theoretical standard deviation of estimates. For the controlled sampling estimate this may be obtained by scaling up the variance of the sampling units and yields a result on the order of $10^3$. Using maximum-likelihood techniques, Bailey (1951, 1952) gives the theoretical variance of the population estimate for the Lincoln method as

$$\text{var}\ \hat{x} = \frac{a^2 n (n - r)}{r^3}$$

in which a = the marked individuals, n = sample size, r = the number of recaptures, and $\hat{x}$ = the estimate of population size. This yields a standard deviation on the order of $10^4$. For Jackson's negative method,

$$\text{var } \hat{x} = \left(\frac{\hat{x}}{n}\right)^2 \left[\left(\frac{\hat{x}\Sigma j^2 a_{(j)}}{(\Sigma j^2 a_{(j)})(\Sigma a_{(j)}) - \Sigma j a_{(j)}}\right) - 1\right]$$

for the $j^{th}$ day where the death rate $= 0$. In this study, the standard deviation for Jackson's negative method is also on the order of $10^4$. This may be assumed likewise for the positive method using the same data.

The population estimates yielded by application of the three capture-recapture methods to the mobile phase and that obtained by sampling the immobile phase lie close together. Since the variances of estimates of the population by the various methods are not homogeneous, testing the estimates on the assumption that they arise from the same population seems inappropriate. The following observations may be made, however.

(1.) The assumptions underlying the capture-recapture methods seem to be met in the mobile phase of *Uca pugilator.*
(2.) Despite the inherently greater variances of the capture-recapture methods, the estimates derived by their use may be more acceptable or preferred to controlled areal sampling estimates on the basis of time and energy investment, as well as of contributing little to disruption of the habitat or of the crabs' behavior.
(3.) The advantage of Jackson's methods over the Lincoln Index lies almost wholly in their ability to allow for changing population size and not on their having greater validity or precision of estimates.

The variances of the capture-recapture estimates are felt to be influenced by several recognizable sources of error. Part of it may be due to variation in environmental properties, such as the amount of cloud cover, the set and velocity of the wind, and the height of the sun as the tidal cycle advances through the daylight hours, which affect the willingness of the crabs to leave the burrows. Part of it is experimental, which is thought to include imprecision in placement of the traps relative both to the site of mobbing activity and to the stage of the tidal cycle, to influences of the presence of the traps upon behavior, to lack of knowledge of the true relationship of the mob to the area sampled during the immobile phase, and to the fact that one sub-population used a promenading area (Fig. 1, D) which was not contiguous to its burrowing area (Fig. 1, 5). A further source of error arises from the fact that the series of the estimates were based upon sub-populations of which varying proportions, from day to day, randomly remained outside the promenading mobs.

We recognize that an increase in the number of crabs captured would have served to reduce sampling error in two ways. First, larger captures would have represented a larger fraction of the population and would have allowed the estimates to be derived with less variance. Second, the importance of unusually large or small marking or recapture values in the Jackson models would have been minimized. In developing technique for sampling, these limitations were tolerated as preferable to the probable effects of: (1) the presence of several investigators in modifying the activity of the mobile phase over an increased time, (2) the effect of delaying collection of the trapped crabs until the rising tide altered the makeup of the promenading mob, and (3) the consequent return of marked crabs to a site different from that at which their behavior had caused their capture.

The Lincoln Index, in this study, was found to best estimate the population size when only successive day data were used. This agrees with the experience of Russell Hunter and Grant (1966) and is to be expected from the assumption of a closed population.

Andrewartha (1961) has pointed out that the examination of the y values of Jackson's methods will reveal indications of gains or losses in the population within the time span of the period of sampling. These indications may be verified by use of Jackson's formulae for gain or loss. No such trends were indicated in the y values computed during this study. This may be taken as further evidence of the appropriateness of the Lincoln Index as used here. No recruitment of mature fiddlers was expected or found during the mark-recapture period. The life cycle precludes this. The lack of clear evidence of mortality in an apparently high density crab population may indicate a scarcity of predatory birds.

The consistent identification of fiddlers with particular promenading mobs demands assumption of retention of this identity during the immobile stage. But, we have also been moved to wonder if the apparently continuously dispersed burrows can be divided either into clean cut segregations or, at least, into concentrations of fiddlers with particular promenading mob allegiances. Only general indications of the boundaries between such groups can be seen in the stratified sampling data, the random scatter of quadrats not having allowed for good linear coverage along the strand. This population of crabs belongs to Crane's (1943) shade-loving category, burrowing almost exclusively among the roots and stolons of *Spartina*. We have some indication that the zone of transition between the burrows of one sub-population and the next may occur where topography reduces or eliminates this cover. There follows, therefore, the inference that the mob is derived from a population occupying a circumscribable burrowing area.

The authors acknowledge with appreciation the contributions of Freda Hockett, who assisted with the field work, Katherine Kritzler, who typed the manuscript and Dennis S. Cassidy who assisted in preparation of the figure.

## Summary

1. Estimates of the size of a population of sand fiddler crabs, *Uca pugilator* (Bosc), were made with the Lincoln Index and Jackson's "positive" and "negative" models in the mobile phase of the activity cycle, and by stratified sampling of the immobile phase.

2. Restricted random sampling was employed because of extremely contagious distribution of the crabs during the mobile phase and of desire to achieve better coverage of the burrowing area than unrestricted random sampling might have yielded during the immobile phase.

3. During the mobile phase, the overall population was divided into four mobs, one separated from the rest by a physical, and the others from each other

by a behavioral barrier. Only three out of 8967 marked individuals were recaptured outside their home territories. Some evidence suggesting that the mobs are derived from subpopulations occupying circumscribable burrowing areas was obtained.

4. Appropriateness of the Lincoln Index was supported by immediate random dispersal of marked crabs among the unmarked mobs, and by failure of the Jackson methods to reveal evidence of population size change during the sampling period.

5. Recognition of the inhomogeneity of variances of estimates obtained by the several methods precluded statistical testing of the estimates on the assumption that they arise from the same population. While it is manifest that all the samples were drawn from the same over-all, isolated population of crabs, it is also obvious that the variance of one estimate was based on spatial distribution, while those of the others were based on behavior. Nevertheless, it was concluded that the assumptions implicit in capture-recapture methods are satisfied during the mobile activity phase of *Uca pugilator* and that for reasons of practicality and preservation of the habitat, these are preferable to estimates of population size by excisive, random, areal sampling during the immobile phase.

6. It is recognized that larger samples would have contributed to more satisfactory validation of the methods, to reduction of variance, and to positive bias. But it was concluded that those which formed the basis of this study were at least adequate, or even preferable, because of probable effects on the crabs' behavior of extended disturbance of mobbing and of the burrowing area.

## LITERATURE CITED


Andrewartha, H. G., 1961. *Introduction to the Study of Animal Populations.* Methuen and Co. Ltd., London, 281 pp.

Bailey, N. T. J., 1951. On estimating the size of mobile populations from recapture data. *Biometrika,* **38**: 293–296.

Bailey, N. T. J., 1952. Improvements in the interpretation of recapture data. *J. Anim. Ecol.,* 21: 120–127.

Crane, J., 1943. Crabs of the genus *Uca* from Venezuela. *Zoologica,* **28**: 33–44.

Crane, J., 1958. Aspects of social behavior in fiddler crabs with special reference to *U. marcacoani. Zoologica,* **43**: 113–136.

Jackson, C. H., 1937. Some new methods in the study of *Glossina morsitans. Proc. Zool. Soc. London,* **1936**: 811–896.

Jackson, C. H., 1939. The analysis of an animal population. *J. Anim. Ecol.,* **8**: 238–246.

Lincoln, F. C., 1930. Calculating waterfowl abundance on the basis of banding returns. *U. S. Dep. Agr. Circ.,* **118**: 1–4.

Miller Don C., 1961. The feeding mechanism of fiddler crabs with ecological considerations of feeding adaptations. *Zoologica,* **46**: 89–100.

Russell Hunter, W., and D. C. Grant, 1966. Estimates of population density and dispersal in the naticid gastropod, *Polinices duplicatus,* with a discussion of computational methods. *Biol. Bull.,* **131**: 292–307.

Tashian, R. E., and F. John Vernberg, 1958. The specific distinctness of the fiddler crabs *Uca pugnax* (Smith) and *Uca rapax* (Smith) at their zone of overlap in North East Florida. *Zoologica,* **43**: 89.